Annals
of the
Missouri Botanical Garden

Vol. 53 1966 No. 1

A CONTRIBUTION TO THE ECOLOGY OF PELAGOPHYCUS[1]

BY BRUCE C. PARKER AND JOHN BLECK

Department of Botany, Washington University, St. Louis, Missouri and
Department of Botany & Plant Biochemistry, University of California, Los Angeles

ABSTRACT

A year-round study of the giant benthic kelp, *Pelagophycus giganteus*, was conducted by scuba diving. Several lines of evidence, including laboratory studies, point to a seasonal temperature-regulated sexual life-cycle for this essentially annual species. Juvenile sporophytes grow faster and have a higher mortality rate than adult, reproductive plants. Most members of he population develop at 70-100 ft depth which receives 5-10% of the surface blue-green illumination, but adult plants at the population's outer periphery (125 ft deep) receive less than 1% of the surface blue-green illumination. Juvenile transplants of the close relative, *P. porra*, do not develop in the natural habitat of *P. giganteus*.

Pelagophycus is a giant lessoniaceous brown alga endemic to the islands and coastal waters of southern California and northern Baja California. Until recently little was known of this relatively inaccessible, deep-water kelp. However, the improvement of scuba diving techniques and increased interest in ocean resources have enabled and encouraged more extensive investigations of this alga in its natural habitat.

Dawson (1962), Parker & Dawson (1964), and Parker & Bleck (1965) studied the systematics and distribution of the three species of *Pelagophycus*. Parker & Fu (1965) compared the anatomy of *P. giganteus* to that of *P. porra* and to *Macrocystis* and *Nereocystis*. Parker & Dawson (1965) described a fossil Miocene kelp from southern California which appears intermediate between *Pelagophycus* and *Nereocystis*. Thus, while the taxonomy and structure of mature, reproductive plants of this genus have been treated, practically no information is available concerning the growth and development of the sporophytic generation. Further, the life-cycle, beyond that reported for *P. porra* by Herbst & Johnstone (1937), is poorly known. Studies along these lines provide a basis for understanding the ecology of

[1] This study was supported, in part, by a grant from the University of California, Los Angeles; we also wish to acknowledge the indispensable assistance of Frances Sizelove of the Glendale Y.M.C.A. and numerous scuba divers of the U.C.L.A. senior diving team.

ANN. MISSOURI BOT. GARD. **53**(1): 1-16, 1966.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **52**, No. 4, pp. 487-604, was published on January 5, 1966.

Pelagophycus, including the longevity of plants, factors affecting distribution limits of the species, and stability of morphological features now used as taxonomic criteria for the species.

The population of *P. giganteus* at Long Point, Santa Catalina Island, California, was selected for these studies because the location (10 mi by land + 20 mi by sea) was the nearest known, undisturbed habitat of *Pelagophycus* to the investigators' laboratory at the University of California, Los Angeles. The objectives of this investigation were designed to meet the limits imposed by (a) distance and sea travel facilities, as influenced by weather conditions, to and from the experimental site, (b) availability of scuba diver personnel, (c) maximum allowable time per diver at a depth of 90 ft, (d) scuba diver proficiency in terms of physical dexterity for measuring and recording data in the natural environment of *Pelagophycus*. With these limitations in mind, we set the following specific goals:

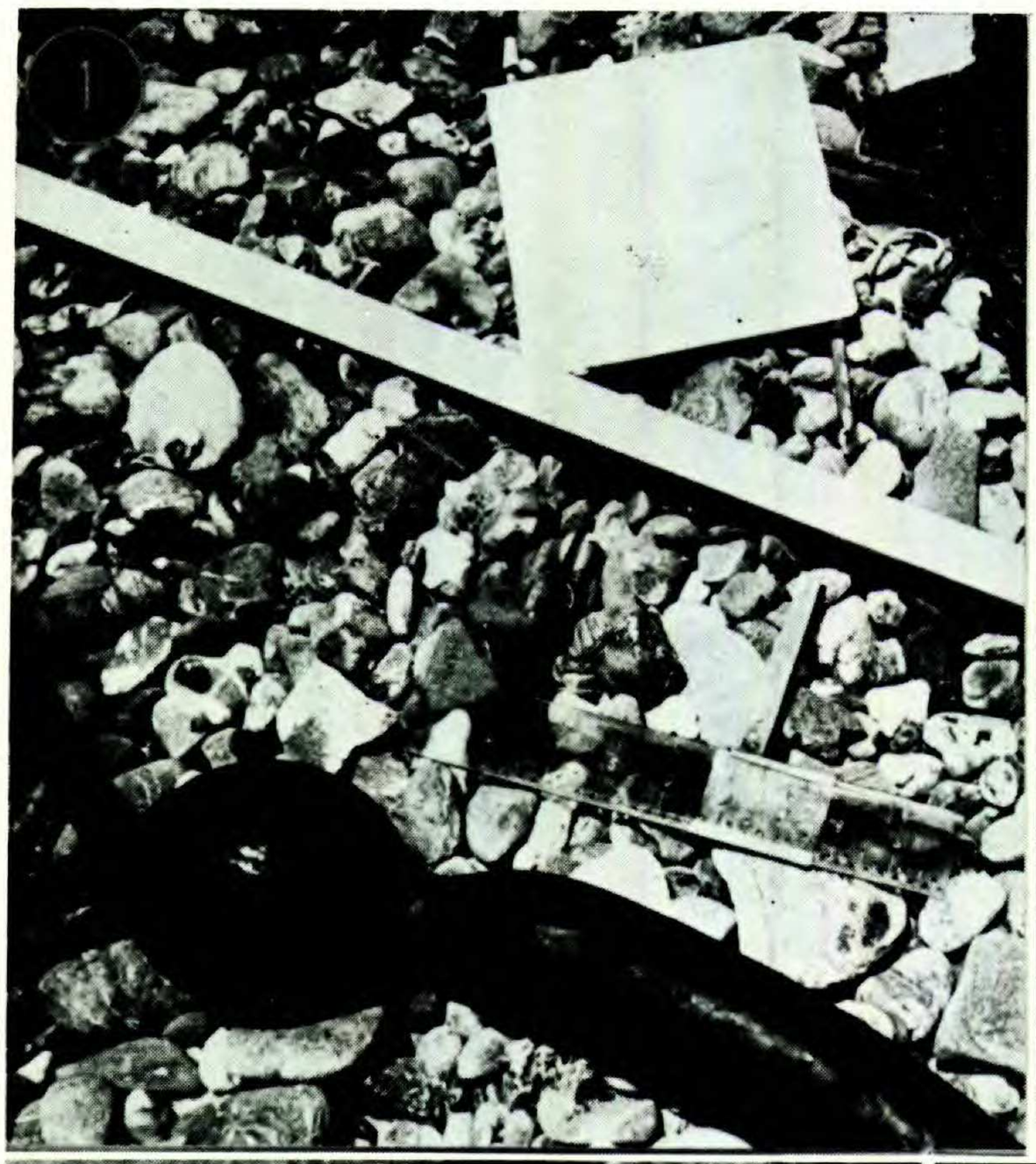
1. To establish two 12 × 50 ft rectangular, submarine plots, tag the plants therein, and make periodic measurements of stipe length, maximum pneumatocyst width, and maximum holdfast diameter in parallel with observations of sporophyte plant development.
2. To measure temperature and light, as time and equipment permitted, at the experimental site during the course of other operations.
3. To transplant juvenile sporophytes of *P. porra* from their coastal habitat to the natural insular habitat of *P. giganteus* at Long Point, Santa Catalina Island, and follow their growth and development.
4. To culture spores of *P. giganteus* and follow their development as a supplement to observations of macroscopic sporophyte development in the natural environment.

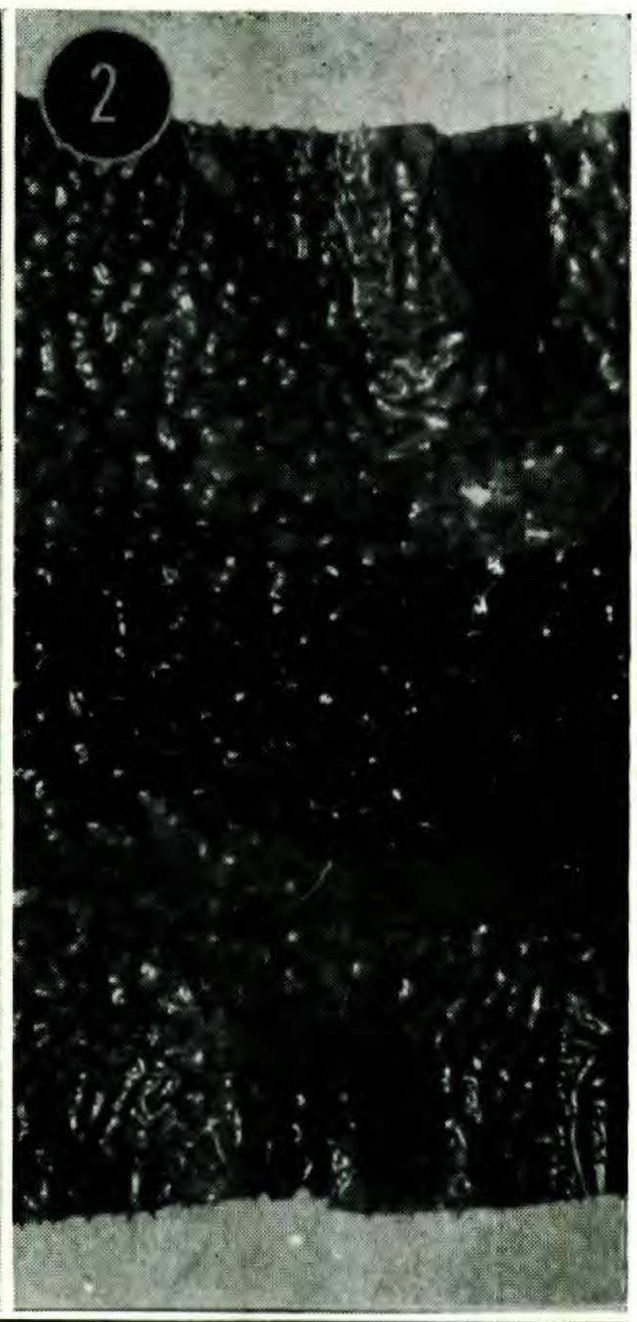
We estimated that the above objectives might be accomplished within 1½ years.

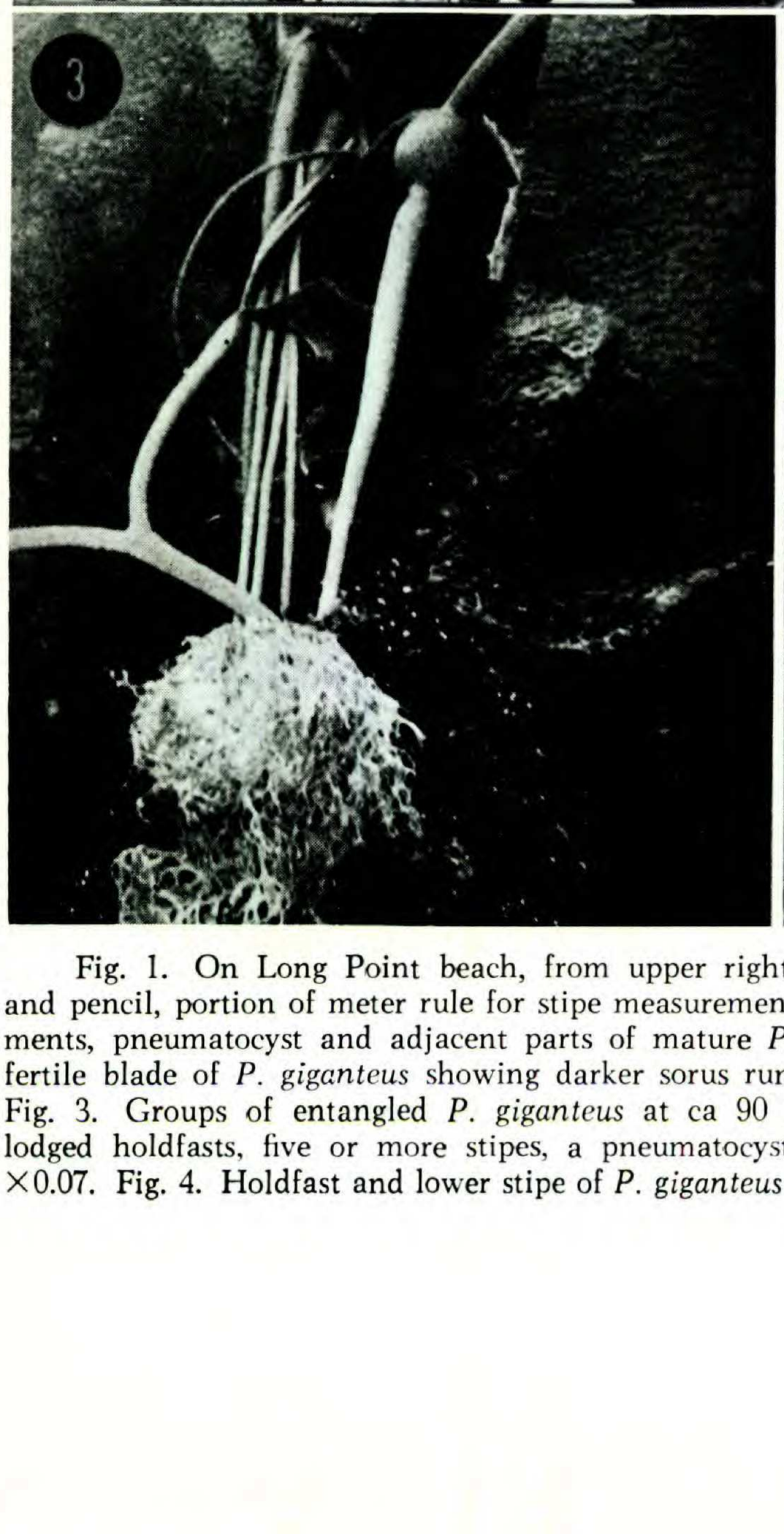
Preliminary Studies and Establishment of Experimental Plots

We obtained transportation and accommodations chiefly from the Glendale, California Y.M.C.A. which maintains a camp at Long Point and operates a 35 ft supply boat to and from the camp site periodically on a year-round basis. Initially two-day visits were planned at least once each month, and on occasions, we had to travel by seaplane or commercial boat to Avalon, Santa Catalina Island, then proceed by special charter boat to Long Point. One of us (J. B.) participated in all dives and directed the submarine operations. A few to many volunteer divers assisted in initiating experiments and collecting data.

Following exploratory dives to evaluate the size and density of the population on February 1, 1964, the two rectangular plots (12 × 50 ft) were demarcated with 12 ft aluminum rods and 50 ft nylon lines; the latter was secured by metal corner stakes. An air-filled, white plastic bottle attached to one corner served as a marker for quick location of plots during subsequent dives. The plots were intentionally established near the center of the *Pelagophycus* population and encompassed about







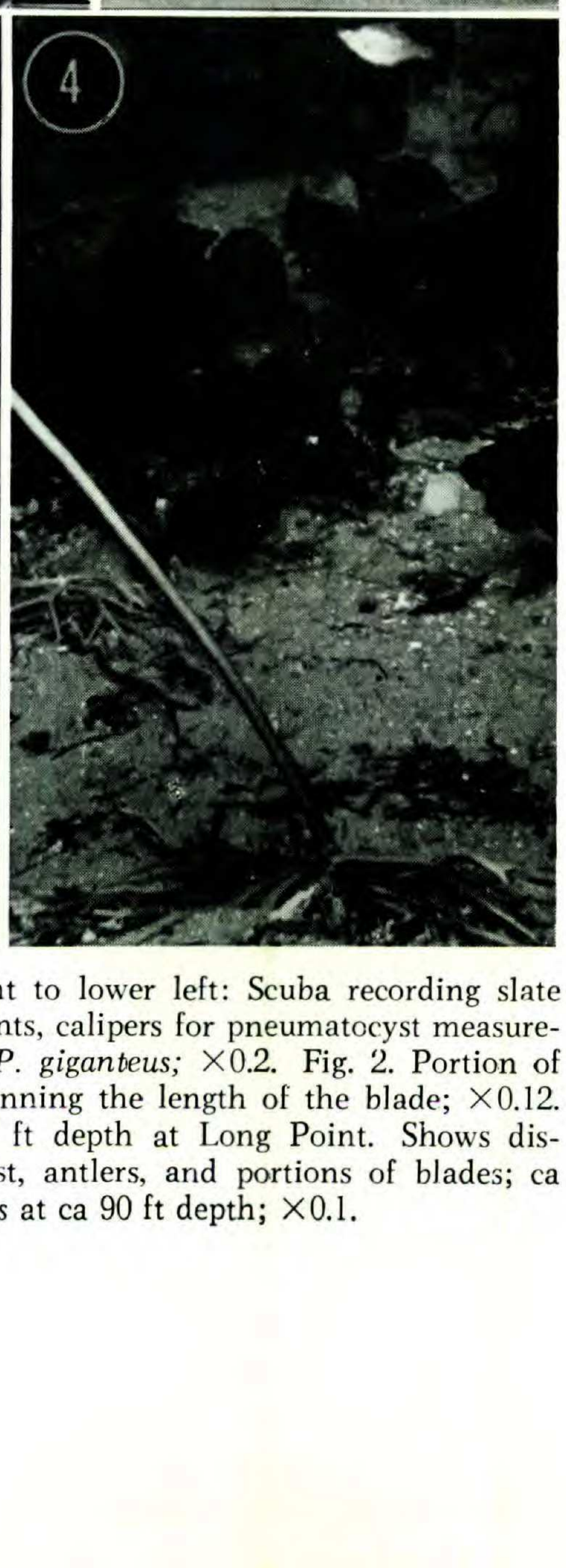


Fig. 1. On Long Point beach, from upper right to lower left: Scuba recording slate and pencil, portion of meter rule for stipe measurements, calipers for pneumatocyst measurements, pneumatocyst and adjacent parts of mature *P. giganteus;* ×0.2. Fig. 2. Portion of fertile blade of *P. giganteus* showing darker sorus running the length of the blade; ×0.12. Fig. 3. Groups of entangled *P. giganteus* at ca 90 ft depth at Long Point. Shows dislodged holdfasts, five or more stipes, a pneumatocyst, antlers, and portions of blades; ca ×0.07. Fig. 4. Holdfast and lower stipe of *P. giganteus* at ca 90 ft depth; ×0.1.

the same number of plants as found in an equivalent area elsewhere in the population (i.e. ca 8 adults/600 sq ft). Plot 1 occurred at 80-85 ft depth, while Plot 2 was located at a depth of 85-90 ft. *Pelagophycus* sporophytes within these plots received a numbered, yellow, plastic tag (ca 1.5 × 3 in) attached with plastic-covered wire just above the pneumatocyst (Fig. 1, 3, 5). In this and all later operations, the divers avoided excessive disturbance of plants and substratum.

The exploratory dives revealed that the entire population of *P. giganteus* at Long Point stretched across the cove for several hundred yards. Occasional plants occurred at about 50 ft and the population continued to a depth of at least 125 ft. These inner and outer boundaries of the population reached a horizontal distance of about 225-300 ft. *P. giganteus* possesses a large flattened holdfast partially buried in the substratum of grey silty sand (Fig. 4). Occasional outcroppings of rocky reefs interrupted the population of *P. giganteus*. The rocks contained a denser community of plants and animals, *Macrocystis pyrifera* being one of the dominants. The less dense *P. giganteus* community contained such seaweeds as *Dictyopteris* sp., *Eisenia arborea* Areschoug, *Laminaria farlowii* Setchell, *Ectocarpus* sp., and several red algae encrusting small pebbles. Some animals frequently observed were *Astraea undosa* (wavy top snail), *Conus californicus* (California cone snail), *Norrisia norrisii* (smooth turban snail), *Tegula aureotincta* (guilded turban snail), *Stichopus parvimensis* (sea cucumber), one or more species of tube anemone (*Ceriantheridae*), *Chromis punctipinuis* (blacksmith fish), *Oxyjulis californica* (Senorita fish), *Paralabrax clathratus* (kelp bass). Some of the larger game fishes *Paralicthys californicus* (halibut) and *Pimelometapon pulcrum* (sheepshead) sometimes lay beneath the massive 35 ft-long blades of *Pelagophycus*. These blades characteristically extended horizontally in the direction of the prevailing current with their distal two-thirds drooping close to the substratum (Fig. 3, 5). The light beneath these blades was drastically reduced.

During our first observations of *Pelagophycus* at Long Point in the late summer and fall of 1963, we rarely encountered juvenile sporophytic plants. Juveniles were still scarce on February 1-2, 1964, which explains why the nine tagged plants in Plot 1 and six tagged specimens in Plot 2 were mature, judging from their blade numbers and other morphological features. One outstanding difference between plants observed on February 1-2, 1964, and those observed and collected during 1963, was the occurrence of reproductive sori on most of the blades of the February plants (Fig. 2).

Measurements of Growth and Development

Initial measurements of tagged plants were made February 8, 1964. Measurements were taken subsequently at approximately 5-week intervals until June 16, 1965, when the study was terminated. Stipe length was determined with a meter rule to the nearest centimeter, while maximum pneumatocyst diameter was determined with calipers (Fig. 1). Measurements by different divers on identical plants within a few minutes of each other never varied by more than 2.8 cm for stipe length, nor more than 0.4 cm for pneumatocyst width. These proved the most reliable measureable features of these giant seaweeds. Blades were too delicate to

be manipulated by divers, and holdfasts, which were initially included in the measurements, proved unreliable due to periodic shifting of the sandy substratum which exposed or covered parts of this organ. All measurements and other observations were promptly recorded on a slate carried by each diver (Fig. 1).

At the time of tagging, plants 3 and 5 in Plot 1 possessed four blades each, while plant 6 had five blades and the remaining individuals had six blades each. All Plot 1 plants had elliptical pneumatocysts (Fig. 1, 5) except No. 2 which had a relatively spherical one (Fig. 3). In Plot 2, plant No. 4 had four blades, Nos. 1 and 5 had five blades each, Nos. 2 and 6 had six blades, and No. 3 had seven blades. All Plot 2 plants had elliptical pneumatocysts except Nos. 2 and 3. Throughout these studies, the numbers of blades on these plants did not change except in the case of Nos. 1 and 5 in Plot 2 which ultimately developed six blades each. The observed initial shape of the pneumatocyst of all tagged plants did not change.

Table 1 contains the data for stipe length and maximum pneumatocyst width. Note that all plants in Plot 1, except No. 9, disappeared within seven months of their initial tagging, while the majority of plants in Plot 2 persisted for more than a year. On June 16, 1965, our last visit to the plots still revealed plants 1 and 2, thus constituting 16½ months from the time of their initial tagging.

The mean increments for the intervals in Table 1 do not represent significant values for the whole population of *P. giganteus* at Long Point. These values, however, indicate the general trends in stipe elongation and pneumatocyst enlargement for mature plants in the plots. The mean increase in stipe length per plant during the entire period of 16 months is approximately 15 cm suggesting an average rate of stipe elongation of nearly 1 cm per month. For the pneumatocyst, the mean increase in maximum width is approximately 0.18 cm which constitutes an average rate of enlargement of 0.01 cm per month.

Some values in Table 1 appear discrepant because they represent decreases in stipe length or pneumatocyst width in excess of that which would be expected to occur through measurement errors. Examples of these and dates of measurement for Plot 1 are, as follows: Plant No. 1 (5-2-64 and 8-2-64), No. 3 (8-2-64), No. 5 (3-28-64), all pertaining to stipe length; No. 9 (5-2-64 and 10-11-64) pertaining to pneumatocyst width. Examples of discrepant figures in Plot 2 are, as follows: Plant No. 4 (5-2-64), No. 5 (6-10-64 and 1-16-65), No. 6 (8-2-64), all pertaining to stipe length; No. 2 (6-10-64), No. 4 (3-28-64 and 6-10-64), No. 5 (1-16-65 and 2-13-65), pertaining to pneumatocyst width.

With respect to stipe length discrepancies, we found that haptera originate continuously through the life of a mature plant. They are produced at the base of the stipe just above the level of the last-formed haptera. Our stipe length measurements include the distance between the uppermost haptera of the holdfast and the pneumatocyst base. Thus, these apparent reductions in stipe length are results of haptera production, and the elongation rates of the stipes as recorded in our tables are probably slightly less than the actual rate of stipe elongation. We were unable to find a reason for the discrepancies in pneumatocyst measurements although the possibility of different gas pressures within this organ has occurred to us.

Table 1. Measurements of stipe elongation and pneumatocyst width expansion (in parentheses) for *Pelagophycus giganteus* adult plants in plots 1 and 2 (all in cm.).

Date	PLOT 1 Plant no.									PLOT 2 Plant no.						Mean Increments
	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	
2-8-64	117 (8.57)	162 (9.30)	200 (7.32)	205 (8.57)	200 (7.62)	210 (8.57)	230 (7.92)	275 (8.57)	132 (7.32)	150 (7.92)	148 (7.92)	154 (8.89)	115 (8.57)	76 (8.25)	90 (7.62)	
3-28-64	120 (8.89)	Gone	200 (7.62)	Gone	190 (8.08)	200 (8.57)	230 (8.57)	275 (8.89)	130 (8.08)	160 (8.41)	155 (8.41)	155 (9.30)	120 (8.08)	75 (8.08)	90 (8.25)	0.23 (0.40)
5-2-64	106 (8.89)		220 (7.62)		190 (7.92)	Gone	230 (8.57)	285 (8.57)	140 (7.62)	160 (8.25)	158 (9.30)	160 (9.19)	110 (8.89)	78 (8.25)	95 (8.89)	2.7 (0.11)
6-10-64	115 (9.04)		225 (7.92)		210 (7.92)		235 (8.57)	300 (9.19)	140 (8.57)	180 (8.89)	170 (8.73)	160 (9.19)	120 (8.57)	70 (8.25)	95 (8.89)	7.3 (0.23)
8-2-64	108 (8.89)		215 (8.25)		215 (8.25)		230 (8.57)	* (9.30)	142 (8.57)	180 (8.89)	175 (9.86)	160 (9.19)	Gone	75 (8.57)	90 (9.19)	—1.0 (0.12)
9-12-64	Gone		Gone		Gone		Gone	Gone	142 (9.19)	187 (9.19)	178 (8.89)	157 (9.30)		77 (8.57)	100 (9.30)	3.2 (0.03)
10-11-64									144 (8.57)	—	180 (9.19)	157 (9.30)		76 (8.89)	100 (9.86)	0.6 (0.13)
11-28-64									140 (8.57)	197 (9.30)	183 (9.19)	161 (9.19)		80 (8.89)	100 (0.16)	2.9 (0.05)
1-16-65									Gone	200 (9.30)	180 (9.19)	161 (9.30)		74 (8.57)	98 (9.86)	—1.6 (—.10)
2-1-65										195 (9.30)	178 (9.19)	158 (9.30)		75 (8.89)	100 (10.16)	—1.4 (0.12)
2-13-65										194 (9.30)	178 (9.19)	160 (9.30)		73 (8.57)	100 (10.16)	0.33 (—.06)
3-20-65										199 (9.30)	176 (9.19)	—		74 (8.57)	100 (10.16)	1.0 (0)
4-24-65										195 (—)	—	158 (—)		74 (—)	Gone	—2.0 (—)
6-16-65										197 (10.16)	178 (9.19)	Gone		Gone		2.5 (0.43)

*Plant dislodged by diver during pneumatocyst measurement.

Sori were abundant on blades of all plants within plots from the beginning of our study in February, 1964, until September, when an obvious reduction in soral area on blades was noted. No juvenile plants occurred inside or in the vicinity of the plots until May 2, 1964, when tiny, barely visible brown algae, presumed to be *Pelagophycus*, made a dramatic appearance. Each plot contained nearly 1000 of these plants. On June 10, 1964, we confirmed the identity of many of these plants which had formed pneumatocysts and antlers characteristic of the genus. Plants were too small and delicate to be tagged and measured during this early stage of development, but we noted that a high percentage of the juveniles had already disappeared. In October, all juveniles remaining in the plots were tagged and measured.

The data for stipe length and pneumatocyst width of the juvenile plants in the plots are recorded in Table 2. Note that only two of the seven tagged juveniles survived until June 16, 1965. Because their origin as macroscopic sporophytes was approximately May 2, 1964, these two remaining plants were approximately one year old. A comparison of the Mean Increments of these plants in Table 2 with those for the mature plants in Table 1 shows that the stipes and pneumatocysts of the juveniles elongated and expanded more rapidly than those of the adult plants. On the average, the stipes of the juvenile plants elongated approximately 10-11 cm per month.

Because we had found so few juveniles in our plots, we sought further data from juveniles by making a 100 ft line transect a few feet north of the two plots. All *Pelagophycus* individuals with holdfasts less than one foot on either side of this line received numbered tags. Measurements were taken, as described previously. The data on stipe elongation and pneumatocyst enlargement for 20 plants along this line transect are recorded in Table 2. These 20 plants perhaps constitute a more heterogeneous sample than the ones located in the plots, because of greater differences in age. However, the Mean Increments show that the rates of stipe elongation and pneumatocyst enlargement were much higher than those for mature plants in the plots. The average rate of stipe elongation for these transect plants was about 6 cm per month. The transect plants were not followed long enough to determine maximum age, but within about four months from the time of labelling, approximately 50% of the sample remained.

Measurements of Light and Temperature

Light measurements were made with a single underwater unit consisting of a Weston self-generating barrier layer cell (Type 856RR) mounted in a water-tight housing.[2] The barrier layer cell was shielded from the water by a braded translucent plastic collector with cosine collecting properties. A Wratten 45 blue-green filter (440-530 mμ, peak at 490 mμ) was used in the underwater unit with one to several Kodak neutral density filters. The barrier layer cell was connected to a 100 microamp meter contained in a transparent plastic housing by water-tight rub-

[2] Construction of light apparatus was based on a design used by Robert L. Holmes, Scripps Institution of Oceanography, La Jolla, California.

Table 2. Measurements of Stipe Elongation and Pneumatocyst Width Expansion of *P. giganteus* Young Plants in Plots 1 and 2 and Transect.

DATES ⟶		10-11-64	11-28-64	1-16-65	2-1-65	2-13-65	3-20-65	4-24-65	6-16-65
	NO. PLT.								
PLOT 1	A02	22 (1.93)	Gone						
PLOT 2	A01	47 (4.45)	73 (5.72)	—	—	92 (6.35)	Gone		
	A03	43 (3.81)	61 (4.78)	62 (4.78)	—	65 (5.08)	Gone		
	A04	44 (4.11)	Gone						
	A05	43 (3.81)	78 (4.78)	95 (4.78)	96 (5.08)	Gone			
	A06	87 (5.38)	136 (6.65)	163 (7.32)	163 (7.32)	161 (7.62)	166 (7.92)	183 —	202 (9.19)
	A07	82 (5.38)	130 (6.35)	140 (6.99)	140 (6.99)	150 (6.99)	155 (7.62)	169 —	192 (8.89)
MEAN INCREMENTS			33.2 (1.15)	13.8 (0.33)	0.33 (0.10)	7.5 (0.31)	5.0 (0.46)	15.5 —	21.0 (1.27)
LINE TRANSECT	D1				157 (5.08)	157 (5.08)	160 (5.38)	170 (5.72)	Gone
	D3				49 (3.48)	48 (3.81)	46 (3.81)	50 (3.81)	Gone
	D4				135 (6.65)	137 (6.35)	148 (6.65)	148 (6.99)	155 (7.62)
	D5				108 (5.08)	111 (5.38)	120 (6.02)	125 (6.35)	138 (7.32)
	D6				266 (5.08)	269 (5.38)	279 (7.32)	— —	314 (7.92)
	D7				211 (7.92)	212 (7.80)	— —	225 (8.57)	229 (9.19)
	D8				195 (—)	Gone			
	D9				192 (6.02)	193 (5.72)	193 (6.02)	204 (6.35)	224 (6.99)
	D10				54 (3.81)	53 (4.45)	56 (4.78)	62 (5.08)	72 (5.72)
	D11				222 (5.72)	223 (6.02)	226 (5.10)	— —	252 (7.32)
	D12				30 (3.18)	32 (2.72)	Gone		
	D13				165 (6.35)	177 (6.99)	191 (7.62)	197 (8.25)	205 (8.57)
	D16				168 (5.72)	— —	191 (6.65)	192 (5.72)	Gone
	D17				30 (3.18)	31 (2.72)	Gone		
	D18				26 (2.84)	28 (2.84)	Gone		
	D19				231 (8.25)	— —	264 (8.25)	286 (8.25)	Gone
	D20				135 (6.99)	Gone			
	D21				33 (3.81)	33 (4.11)	33 (4.11)	35 (4.22)	35 (4.45)
	D23				48 (3.81)	50 (3.48)	49 (3.48)	Gone	
	D25				110 (6.35)	115 (6.35)	120 (6.99)	125 (7.62)	Gone
MEAN INCREMENTS						1.75 (0.06)	5.57 (0.37)	7.73 (0.15)	13.6 (0.69)

Table 3. Surface and bottom temperatures recorded with bathythermograph at Long Point.

Date	Temperature, C° Surface	25 Meters	Date	Temperature, C° Surface	25 Meters
2-1-64	14.7	14.7	10-11-64	19.4	16.5
2-8-64	14.4	14.4	11-28-64	14.9	14.2
3-28-64	14.4	14.4	11-29-64	14.9	14.5
5-2-64	14.7	14.4	12-20-64	13.3	13.0
6-10-64	17.2	12.0	1-16-65	12.5	12.4
7-9-64	18.1	16.2	1-17-65	13.5	13.2
7-10-64	18.0	11.4	2-1-65	13.5	13.5
7-11-64	18.5	15.0	2-2-65	13.5	13.0
7-12-64	18.5	11.9	2-13-65	13.5	13.0
7-25-64	20.1	13.9	2-14-65	13.3	13.0
7-26-64	19.5	12.9	4-24-65	15.3	15.0
8-1-64	21.5	14.0	6-15-65:		
8-2-64	21.2	13.5	8:00am	16.2	14.0
9-12-64	19.9	16.9	12:00	16.0	14.0
10-10-64	20.0	17.2	4:30pm	15.8	13.5
			8:00pm	15.8	12.5

ber wire couplings. For underwater measurements, the equipment was carried by diver to the plots and read directly at the level of *P. giganteus* blades (ca 80 ft depth). Prior to each set of bottom measurements, a cap containing one or more additional neutral density filters was placed over the photo-cell housing and a reading of the surface blue-green illumination was made. Subsequently, all filters and filter combinations were calibrated in full sunlight at the authors' laboratory using a thermopile as described by Bulpitt *et al.* (1965).

The underwater apparatus was completed in November, 1964. Therefore, our data is not complete for the year-round study and our results must be limited to a few brief statements.

Considerable variation occurs in the percentage of surface blue-green illumination penetrating to the depth of our experimental plots. On January 17, 1965, as little as 2.6% of the surface midday blue-green illumination penetrated to the plots. This constituted approximately 2382 ergs sec^{-1} cm^{-2}. Our highest reading was recorded March 20, 1965, at 11.45 am, when about 24% of the surface blue-green illumination (ca 23,000 ergs sec^{-1} cm^{-2}) reached the blades of the tagged plants. The average of our monthly, midday, bottom readings between November, 1964, and June, 1965, is approximately 8% of the surface blue-green illumination. The illumination beneath blades of *Pelagophycus* was consistently too small to be detected by our equipment.

On February 2, 1965, a deep dive was made to the outer periphery of the *P. giganteus* population at Long Point. The population extended to about 125 ft depth where the irradiance constituted 0.7% of the surface blue-green illumination.

A bathythermograph was used for temperature measurements from surface to depth of the experimental plots. The surface and bottom temperatures are recorded in Table 3. From February 1 to May 2, 1964, the surface and bottom temperatures were approximately the same (ca 14.5 C). This same condition prevailed between November 28, 1964 and April 24, 1965. However, the period from June to October,

1964, included higher surface temperatures than bottom temperatures. This summer period was characterized also by a thermocline (i.e. mixed layer), the depth of which changed hourly and daily. On occasions the thermocline reached 75 ft depth, creating drastically different temperatures for the blades and pneumatocysts of plants which extended into the epilimnion and the stipes and holdfasts located in the hypolimnion. However, generally the thermocline occurred at or above 55 ft depth at Long Point which lay above most of the population of *P. giganteus*.

TRANSPLANTING OF P. PORRA JUVENILE SPOROPHYTES TO LONG POINT

Preliminary to the transplanting experiment, a mature *P. giganteus* specimen was detached from the substratum and pulled to the surface. After 24 hr at the surface, this plant was returned to the bottom at about 80 ft where the holdfast was covered with the silty-sandy substratum. This plant remained several months intact and exhibited no damage to pneumatocyst or other parts. On the success of this venture, 105 juvenile *P. porra* sporophytes were collected from depths of 40-75 ft off La Jolla, California. The smallest specimens had no pneumatocysts, while the largest ones had pneumatocysts up to 6 cm in maximum width, all being spherical. Except for six of the plants which had four blades, all others had one or two blades. All plants were stored nearly 48 hr in circulating seawater tanks at Scripps Institution of Oceanography, then placed into wet burlap sacks and transported 125 mi to San Pedro, California. The sacks were immersed in the sea overnight, and then taken by boat to Long Point. Thus 72-96 hr following collection, the 105 juvenile *P. porra* specimens were replanted. Near the two experimental plots of *P. giganteus*, a 50 ft nylon line was stretched out and secured by aluminum stakes. Large native seaweeds were removed from an area 3 ft to either side of this line. The juvenile *P. porra* plants were then planted along the line at approximately 3 ft intervals. At least 20 of the transplants were still attached to their rocks, as is characteristic of the species; these needed no further attachment. The remaining unattached specimens were fastened to the sandy-silty substratum by two large wire pins, each bent in the shape of a hair pin and inserted through the holdfast at opposing angles with the two prongs anchored in the substratum. Each specimen had a small plastic tag secured to it prior to planting. The transplanting was accomplished on December 19-20, 1964, during very rough weather with some bottom turbulence.

The day after the transplanting, a brief visit to the site revealed that approximately 10 specimens with the smaller holdfasts had been lost during the bottom turbulence. An additional 20 or so plants with 3-6 cm pneumatocysts lay on the bottom, their pneumatocysts collapsed and broken.

The site was next visited on January 16, 1965. Only two of the transplanted *P. porra* sporophytes had survived intact. These two had been among the smallest specimens and lacked well-developed pneumatocysts. Measurement showed that none of the organs had grown during the four weeks at Long Point. The remaining plants had imploded pneumatocysts and/or lacked intact blades. Their holdfasts, stipes, and antlers were intact.

Laboratory Cultivation of Zoospores and Gametophytes of P. giganteus

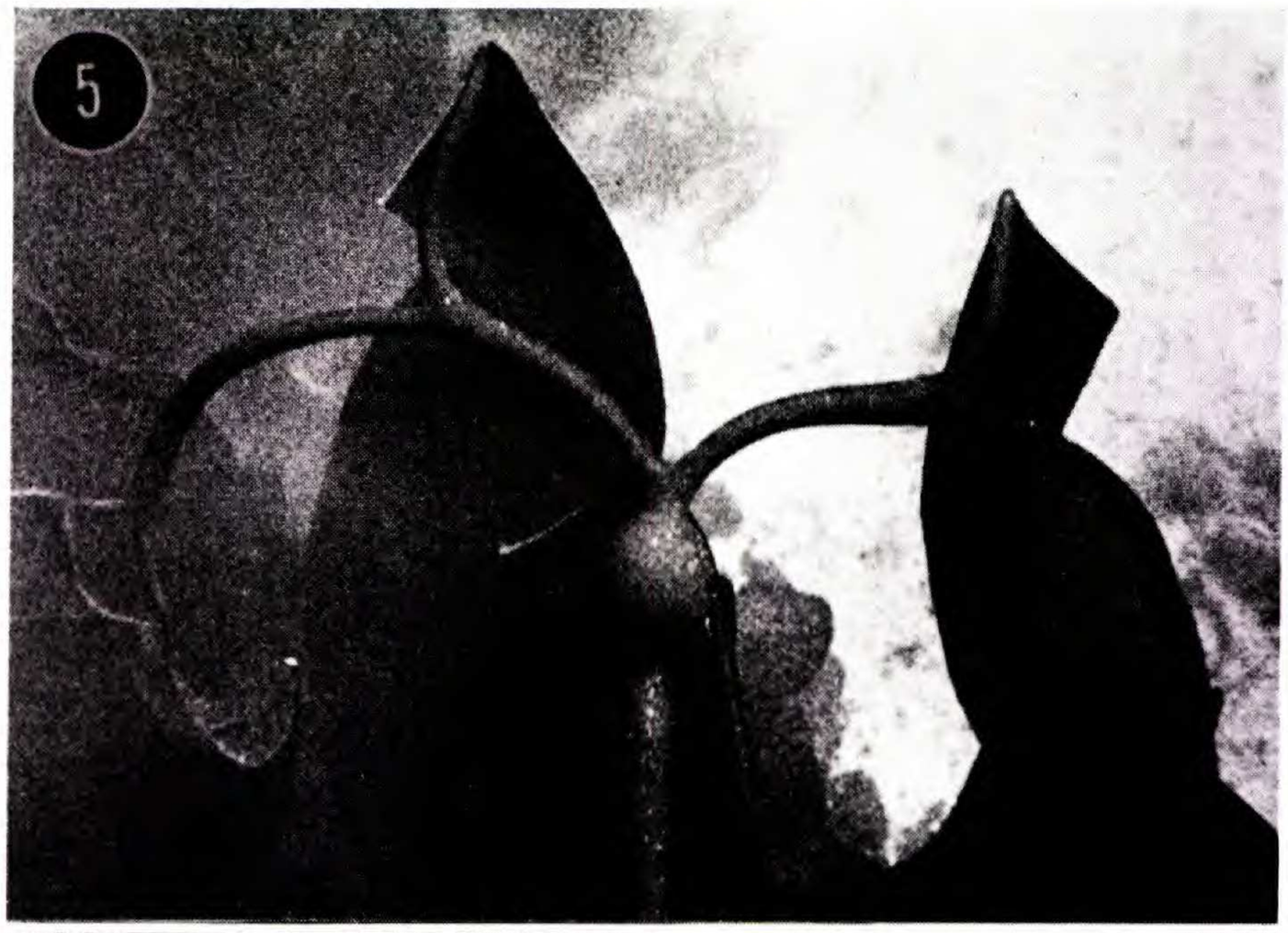
Pieces of sporophylls of *P. giganteus* were brought to the laboratory on February 2, 1964. Following 48 hr storage at ca 5 C in a refrigerator, square centimeter pieces of sori were cut, washed in sterile seawater, and placed in Petri dishes containing autoclave-sterilized enriched seawater medium (Parker, 1965). Cultures were maintained at 10 C under 50-200 ft-c constant illumination from cool-white fluorescent lamps. Microscopic observations of the contents of dishes were made daily.

Twenty-four hr after immersion of soral pieces into the medium, cultures were teeming with biflagellate zoospores, each 4 × 5 μ. About 32 zoospores continued their emergence from certain unilocular zoosporangia. Zoospores were typically reniform with laterally inserted flagella, one projecting anteriorly and the other posteriorly when swimming unidirectionally (Fig. 6). Soral pieces were removed after 48 hr and aliquots of culture liquid containing spores were transferred to fresh, sterile media, and subsequently maintained at 14.5 C (the measured temperature of the natural environment of *P. giganteus* at Long Point). This was considered zero time.

Two days later, motility of zoospores had ceased and spherical cells with rigid walls and several plastids were abundant on the bottom of Petri dishes. Cultures eight days old still contained many single cells, most of which had enlarged to 6 μ or more. By 18 days, 2-, 3-, and 4-celled germlings were common (Fig. 7), and by the end of 28 days, 8- to 12-celled germlings had developed. At this point, a number of larger germlings (12 or more cells) were transferred to fresh media. Forty days after inoculation of zoospores, these germlings had become multibranched filaments of more than 100 cells. The cells of some germlings appeared smaller than those of others within the same culture, calling to mind the distinction into micro- and megagametophyte made by Herbst & Johnstone (1937) in their study of the *P. porra* life cycle. A few of the larger-celled germlings possessed enlarged terminal cells resembling oogonia of *P. porra*. The fate of these enlarged cells was not ascertained, and cultures were again transferred. By the end of 60 days, presumed sporophytes consisting of short uni- and multiseriate filaments of cells appeared in cultures. These were both free-floating and attached to the germlings which had smaller cells (Fig. 8). Following another transfer into fresh media and by 90 days (May 2, 1964), a few presumed sporophytes had developed monostromatic blades of several hundred cells with rhizoids at the base (Fig. 9). Further development of sporophytes within our cultures could not be induced although a variety of methods were tried including shaking the flasks and planting in sterile sand or soil.

Discussion

Our studies of *Pelagophycus giganteus* at Long Point for approximately 1½ years have indicated that a seasonal regulation of the life-cycle of this giant benthic seaweed takes place. This conclusion is supported by a sequence of observations, as follows: (1) Only adult plants constituted the population between the late fall of 1963 and May, 1964; (2) Sporophylls first appeared in February, 1964; (3) A spon-



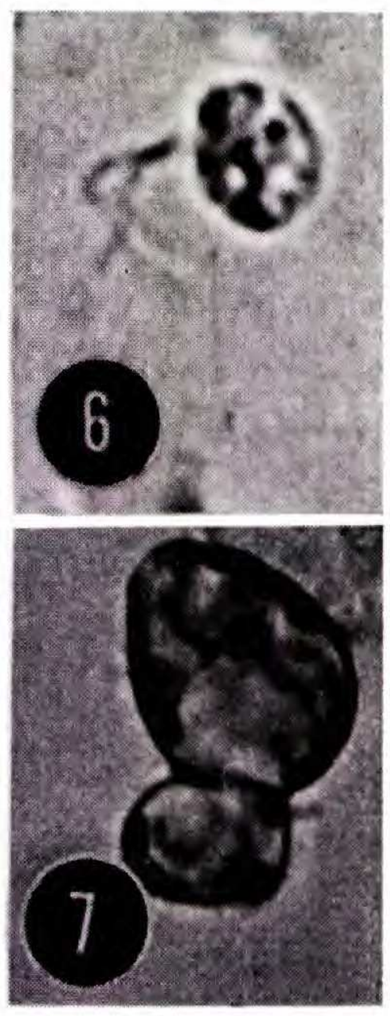


Fig. 5. Upper portion of *P. giganteus* at ca 90 ft depth at Long Point, showing upper stipe and pneumatocyst, antlers, and six blades in their typical drooping habit; ca ×0.1. Fig. 6. Biflagellate zoospore of *P. giganteus;* ×1800. Fig. 7. Two-celled gametophyte, 18 days after release of zoospores; ca ×1800. Fig. 8. 60-day-old gametophytes in culture with predominantly uniseriate sporophytes (larger cells); ×425. Fig. 9. Two monostromatic sporophyte blades of *P. giganteus* attached to female gametophytes after 90 days of culture; ×100.

taneous appearance of tiny sporophytes occurred in May, 1964; (4) Our cultures of zoospores developed into microscopic germlings resembling gametophytes of other *Laminariales* (Fritsch, 1945), and produced macroscopic sporophytes within 90 days, a length of time which coincided with the first appearance of sporophytes in the natural environment. *Nereocystis luetkeana*, a close relative of *Pelagophycus*, also has a seasonal production of sporophylls and juvenile sporophyte plants (Frye, 1906; Rigg, 1917; Setchell, 1908; McLean, 1962).

We have no reasons from our observations of unilocular sporangia, zoospores, germlings, and young sporophytes to suppose that *P. giganteus* has not a normal sexual life-cycle representing heteromorphic alternation of diploid sporophytic and haploid gametophytic generations. Our observations of morphology and the sequence of events resemble closely the life-cycles of *Macrocystis* and *Nereocystis* (Scagel, 1947) as well as that of *Pelagophycus porra* (Herbst & Johnstone, 1937). The germlings are quite likely gametophytes although this conclusion is not irrefutable without further observations of meiosis and gametogenesis.

Numerous factors doubtless play a role in regulating the production of sporophylls, release of zoospores, development of gametophytes, gametogenesis, fertilization, and subsequent development of the young sporophyte generation, but the most influential factor suggested by our studies was temperature. The lowering of the water temperature to 15 C or less appears to have triggered the differentiation of sporophylls and subsequent phenomena which occurred during the winter and spring of 1964. Long Point water temperatures during the late spring and summer of 1964 were abnormally cool compared with previous unpublished reports for the several preceding years. Consequently sporophylls continued their production of spores throughout the summer until September when the water temperature at the level of *P. giganteus* finally rose above 15 C. The temperature of 14.5 C in both natural environment and our laboratory cultures was suitable for development of germlings and at least a limited number of very young sporophytes. These temperatures are somewhat above those (8-12 C) shown to be optimal for germling (also assumed to be gametophyte) development in *P. porra* from the cooler coastal waters near San Pedro, California (Herbst & Johnstone, 1937).

It is noteworthy that several earlier workers arrived at a similar temperature-regulated life-cycle theory for other *Laminariales*. Schreiber (1930) found that lowering the water temperature to 4-6 C induced gametogenesis, whereas raising the temperature to 18 C suppressed this process in *Laminaria*. Hartge (1928) cultured *Nereocystis* at 16 C. Myers (1925, 1928) and McKay (1933) considered 12-16 C optimal for growth and reproduction of *Nereocystis*, and noted that gametophytes developed at 4 C but failed to produce gametes at 12-20 C. Fritsch (1945) further substantiates that the development of sori ". . . usually coincides with the cold season, and the fertile parts often persist through a considerable part of the winter."

Our data have revealed that a high mortality occurs among juvenile *P. giganteus* sporophytes in the natural environment, and that those plants which do survive to a reproductive stage generally do not live beyond that year. This demonstrates that *P. giganteus* is, for the most part, an annual plant. A few individuals tagged in

our study, which had mature, reproductive sporophylls initially, lived for more than a year. These plants in Plots 1 and 2 were apparently at least 6 months old when first tagged, so it is possible that some individuals survive two reproductive seasons and a few may reach two years of age.

Pelagophycus porra and *Nereocystis luetkeana* are also annual plants (Setchell, 1912), while *Macrocystis* is generally considered a perennial (Scagel, 1947), its individual fronds being of a seasonal or annual nature (North, 1961).

Our data on stipe elongation and pneumatocyst enlargement, indicate that the plants first tagged in Plots 1 and 2 were fully grown and subsequently grew at relatively slow rates. In contrast, the younger individuals tagged grew at rates 6-10 times as fast as the mature plants. Unfortunately the delicate construction of very small juveniles and the relatively clumsy techniques which are an inevitable accompaniment to scuba diving prevented our obtaining data on the growth rates of very young sporophytes within the Long Point population.

Our light measurements are only approximations but suggest that 5-10% of the blue-green illumination at the surface penetrates to the depth of 80 ft near the center of the population of *P. giganteus*. This population continues further to 125 ft depth where the blue-green light is reduced to less than 1% of that at the surface. It must be realized that these approximate percentages represent blue-green light only. It is, therefore, meaningless to compare our data with that from laboratory studies. For example, Neushul & Haxo (1963) found that sporophytes of *Macrocystis* required a minimum of approximately 600 lux of continuous, fluorescent light to develop. Our data do not permit us to calculate the total downwelling irradiance, nor to equate this spectral diurnal illumination at 125 ft with the full spectrum of constant illumination used by these workers. Further examination of the light energy reaching *Pelagophycus giganteus* in nature and in laboratory will, no doubt, help define its limits more precisely.

Of interest in connection with adaptation of *Pelagophycus* to low light requirements is an observation we first made while collecting specimens of *P. giganteus* at San Clemente Island during 1963. Plants taken from a depth of 125 ft were chocolate in color, while plants collected at 90 ft or less were lighter brown, presumably due to differences in concentration of fucoxanthin. All plants were approximately the same size with approximately equal total blade surface areas. Obviously the ability of seaweeds to tolerate smaller amounts of light energy also may relate to the total area of photosynthetic surface per individual plant. We note, therefore, that McLean (1962) reported the typical *Nereocystis luetkeana* adult possessed a total blade surface area of 70 sq ft; mature *Nereocystis* blades usually float at the surface. In comparison, *P. giganteus* adults typically possess about 360 sq ft of total blade surface at a depth of 70 ft (data from Parker & Dawson, 1964). A more exhaustive study of photo-synthetic surface area for a variety of marine algae at different depths has not, to our knowledge, been made.

The attempted transplanting of *P. porra* from its coastal habitat to the Long Point habitat of *P. giganteus* was for the most part unsuccessful, yielding little information. No doubt many of the transplants died as a result of imploded pneumatocysts. This probably was caused by a reduced pressure of gases in the

pneumatocysts when the plants were collected and maintained at the surface for 72 or more hours before being returned to a depth of 80 ft or more. Neushul & Haxo (1963) encountered similar difficulties in their transplanting attempts with *Macrocystis*. However, a number of ours smaller plants lacked well-developed pneumatocysts and therefore could not have failed to grow because of injury to this organ. Neither was there any clear indication of excessive grazing of the *P. porra* plants by animals. Two plants whose blades remained intact for four weeks showed no signs of growth in either stipe length or pneumatocyst diameter. This suggests that had the other plants remained intact, they too probably would not have grown. We, therefore, draw the tentative conclusion that *P. porra* cannot develop in the environment of *P. giganteus*, and our evidence thus confirms that these are two distinct species, and not merely ecophenes.

If the germlings which developed from the zoospores were gametophytes, as we suspect, then *P. giganteus* has the kind of heteromorphic alternation of generations which is typical of other members of the *Laminariales*. The spores released were biflagellate and actively motile, in contrast to those of *P. porra* which, accord- to Herbst & Johnstone (1937), were non-flagellated. Also, the zoospores of *P. giganteus* were $4 \times 5\ \mu$, while those of *P. porra* were $3.5 \times 4.0\ \mu$ in diameter. This difference in size, although seemingly small, constitutes a two-fold difference in the calculated volumes of these respective spores; the zoospores of *P. giganteus* are approximately twice the volume of spores of *P. porra*. This suggests to us that the nuclear volumes of these species may also be different by a factor of 2. This has already been reported by Parker & Fu (1965) who found that the nuclear volumes of *P. giganteus* meristoderm cells were precisely twice that of *P. porra* meristoderm cells. They concluded that *P. giganteus* might be a polyploid species derived from *P. porra*. Our observations of germling development and sporophyte production are, primarily, like those reported by Herbst & Johnstone (1937) for *P. porra*, and hence, require no further discussion here.

These investigations have contributed to our understanding of the ecology of *Pelagophycus*. They have answered a number of important questions about this genus and have pointed the way to further areas of fruitful investigation of benthic seaweeds using the scuba diving technique.

Literature Cited

Bulpitt, T. H., M. W. Coulter, & K. C. Hammer. 1965. A spectroradiometer for the spectral region of biological photosensitivity. Appl. Op. **4**: 793-797.

Dawson, E. Y. 1962. On the recognition of a second species of the genus *Pelagophycus*. Bull. So. Calif. Acad. Sci. **61**: 153-160.

Fritsch, F. E. 1945. The structure and reproduction of the algae. Vol. 2, 1-939. Cambridge Univ. Press.

Frye, T. C. 1906. *Nereocystis luetkeana*. Bot. Gaz. **42**: 143-146.

Hartge, L. A. 1928. Nereocystis. Publ. Puget Sound Biol. Sta. **6**: 207-237.

Herbst, C. C. & G. R. Johnstone. 1937. Life history of *Pelagophycus porra*. Bot. Gaz. **99**: 339-354.

McKay, H. H. 1933. Life history of *Pterygophora californica*. Univ. Calif. Publ. Bot. **17**: 111-148.

McLean, J. H. 1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. Biol. Bull. **122**: 95-114.

Myers, M. E. 1925. Contributions towards a knowledge of the life-histories of the *Melanophyceae*. A preliminary report. Univ. Calif. Publ. Bot. **13**: 109-124.

———. 1928. Life-history of the brown alga, *Egregia menziesii*. Univ. Calif. Publ. Bot. **14**: 225-246.

Neushul, M. & F. T. Haxo. 1963. Studies on the giant kelp, *Macrocystis*. I. Growth of young plants. Amer. Jour. Bot. **50**: 349-353.

North, W. J. 1961. Life-span of the fronds of the giant kelp, *Macrocystis pyrifera*. Nature **190**: 1214-1215.

Parker, B. C. 1965. Translocation in the giant kelp *Macrocystis*. I. Rates, direction, quantity of C^{14}-labelled products and fluorescein. Jour. Phycol. **1**: 41-46.

———, & J. Bleck. 1965. A new species of elk kelp. Trans. San Diego Soc. Nat. Hist. **14**: 57-64.

———, & E. Y. Dawson. 1964. Notes on variability and range in the elk kelp *Pelagophycus*. Trans. San Diego Soc. Nat. Hist. **13**: 303-307.

———. 1965. Non-calcareous marine algae from California miocene deposits. Nova Hed. X(1 + 2): 273-295, *pl. 76(1)-96(21)*.

———, & M. Fu. 1965. The internal structure of the elk kelp (*Pelagophycus* species). Canad. Jour. Bot. **43**: 1293-1306.

Rigg, G. B. 1917. Seasonal development of bladder kelp. Publ. Puget Sound Biol. Sta. **1**: 308-318.

Scagel, R. F. 1947. An investigation on marine plants near Hardy Bay, B.C. Prov. Dept. Fish., Victoria, B.C., No. 1: 1-70.

Schreiber, E. 1930. Untersuchungen über parthenogenesis, geschlechtsbestimmung und bartardierungsvermögen bei Laminarien. Planta **12**: 331-353.

Setchell, W. A. 1908. *Nereocystis* and *Pelagophycus*. Bot. Gaz. **45**: 125-134.